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Electrofishing: Fish Reactions with Neurophysiological Explanations

by Pierre Lamarque

Over a number of years, studies in various countries, primarily Germany, have shown that electrofishing could be a valuable aid in pisciculture and hydrobiological studies[1]. Direct current is very often used. An electric field is created in the water, with, for instance, the anode consisting of a copper ring, 40 cm in diameter, attached to the end of a handle. The cathode is placed at the bottom of the water near the generator. Normally the fish are attracted to the anode (anode or positive galvanotaxis), then immobilized (galvanonarcosis). At this stage they can be scooped up in a dip net without any trouble. With a 2-to-3-ampere direct current of 400 volts supplied by a portable generator under average conduction conditions in water, fish are attracted within a 2-to-3-meter radius. Behaviour varies with the species and size. Large fish are more easily attracted than small ones, which is useful for the usual objectives, i.e., sample-taking of breed fish, removal of large pike, tagging, and count-taking, etc.

In order to ensure the full effectiveness of this technique, it was important to elucidate the mechanisms governing the reactions of the fish. The Applied hydrobiology laboratory (Laboratoire d'Hydrobiologie appliquée) in Biarritz has been working on this problem since 1959. In this paper, we have discussed our main findings[2].

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1 See: Freshwater electrofishing by L. Perruche. **La Nature** , March 1957, 88-90.

None of the hypotheses put forward since the beginning of this century satisfactorily explain fish behaviour in an electric field. Some authors suggested a direct action on the muscles, while others attributed the behaviour to excitation of the higher nerve centres, especially via the inner ear. Still others favoured a "psychological" explanation with the fish adopting in the field the position causing them the least discomfort. The authors did not even agree on how certain reactions proceeded or whether they even existed. Cathode galvanotaxis, for example, where in some situations the fish swim toward the cathode, was discovered at the end of the last century but seems to have been given no further notice.

Apparently, this was partially due to the fact that most of the early investigators used alternating currents which induced phenomena that were harder to analyse. They doubtless opted for this approach because of the concepts of electrophysiology then in vogue. It was held that excitation of nerves or muscles could occur only when a circuit was opened or closed. It could not be maintained by the prolonged passage of direct current. This flew in the face of all the evidence as anyone can check out by placing his tongue between the two electrodes of a pocket battery or by sticking his hand in a direct electric field. The persistence of the sensation and, if the potential is high enough, of tetany provides proof that excitation will continue as long as direct current is applied. As early as 1936, the experiments of Professor

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[2] Neurophysiological study of electrofishing (direct current) by M. Blancheteau, P. Lamarque, G. Mousset and R. Vibert. 1 vol. 15.5 x 24, 108 pp., 15 figures. From **Bulletin du Centre d'études et de recherches scientifiques de Biarritz** , 1961. Mention should also be made of a 16-mm film with sound track and colour, lasting roughly 20 minutes to appear shortly: Electricity-Induced Taxis, Narcosis and Tetany in Fish (Taxies, narcose, tétanies électriques chez les poissons) (Scientific Research Film Service - Service du Film de recherche scientifique, 96 boulevard Raspail, Paris 6e).

Fessard on nerves and of Professor Monnnier on muscles gave a scientific basis to these observations.

While the study we conducted with direct current proved complex, work with indirect current poses even greater problems since numerous parameters, such as the frequency and duration of the impulses, come into play. As a result, a number of reactions are masked. A further complication is the vague terminology employed to describe the reactions even with direct current. By way of example, the term 'anode galvanotaxis' was used for two types of reactions involving different nerve structures. As we shall see later, we were able to distinguish between the two, referring to one as 'forced swimming' and to the other as 'pseudo-forced swimming'. The fact that low voltages could inhibit swimming in fish facing the anode was also overlooked (Table 1).

Fig. 1. Electrofishing in the Nivelle River at Saint-Pée (Basses Pyrénées). The man in the middle carries the positive electrode while his helpers follow and catch the fish with dip nets. The negative electrode is 300 m upstream near the generator.

forced swimming

Fig. 2. With a difference of 18 volts between the ends of the tank, the trout swam vigorously to the anode.

Fig. 3. At the Applied hydrobiology laboratory (Biarritz centre for scientific studies and research).
The fish are placed in a plastic tank, 1.20 m in length. Batteries are capable of delivering 2 to 60 V and dynamos, 60 to 1 200 V.

Table 1. Electric Current-Induced Fish Reactions Identified in Biarritz

Current voltage ([1])	Fish facing: the cathode (-)	The anode (+)
10 V	initial reactions without galvanotaxis	
14 V	cathode galvanotaxis([2]) (Fig. 13)	inhibition of swimming([2]) (Fig. 8)
15 V	onset of stiffness	
18 V	stiffness	forced swimming (Fig. 9)
40 V	tetany (Fig. 14)	galvanonarcosis (Fig. 10)
90 V	tetany (Fig. 14)	onset of stiffness pseudo-forced swimming (Fig. 11)
150 V	tetany (Fig. 14)	tetany (Fig. 12)

([1]) Potential differences between the ends of a 120-cm-long tank containing a 20-cm-long trout.
([2]) Cathode galvanotaxis and inhibition of swimming were demonstrated by clocking swimming time with and without the electric current. The results were statistically compared.

The reactions of a fish in a direct electric field therefore vary more than originally assumed. As will be shown, they depend primarily on the position of the nerve fibers in the field, the length of these fibers, and lastly, the potential difference of the field, which gives rise to specific levels of reaction by stimulating or inhibiting different nerve and muscle fibers. In order to understand these mechanisms, it is important to be able to visualize the nervous system of a fish, as diagrammatically shown in Fig. 4.

Table 1 lists the main reactions we identified in Biarritz and Figures 7 to 15 show photos illustrating these reactions. In these photos, the behaviour of the fish is partially represented by the shape and amplitude of the eddies produced by the fish. The eddies are seen far more clearly on photos than on direct observation because of the reflections made by a properly aimed flash.

Nerve Fibers in the Electric Field

Let us first consider the nervous system of the fish body posterior to the the brain (Fig. 4). The spinal cord contains two nerve tracts which run the length of the body. The sensory nerve tract, AB, consisting of short nerve fibers, is connected via the brain (reflex centres Rc) to motor chain CD consisting of long fibers which extend uninterrupted from C (in the medulla) to the tail of the fish. We know that each fiber can be stimulated by a normal impulse in one and only one direction, i.e., from the cell body to the opposite end (terminal endings). This is schematically shown in Fig. 4, to the right. Throughout the following description, when reference is made to AB, CD, etc. or a fiber or nerve tract, it will be remembered that the impulse flows only from A to B and from C to D, etc. The sensory tract can therefore conduct impulses

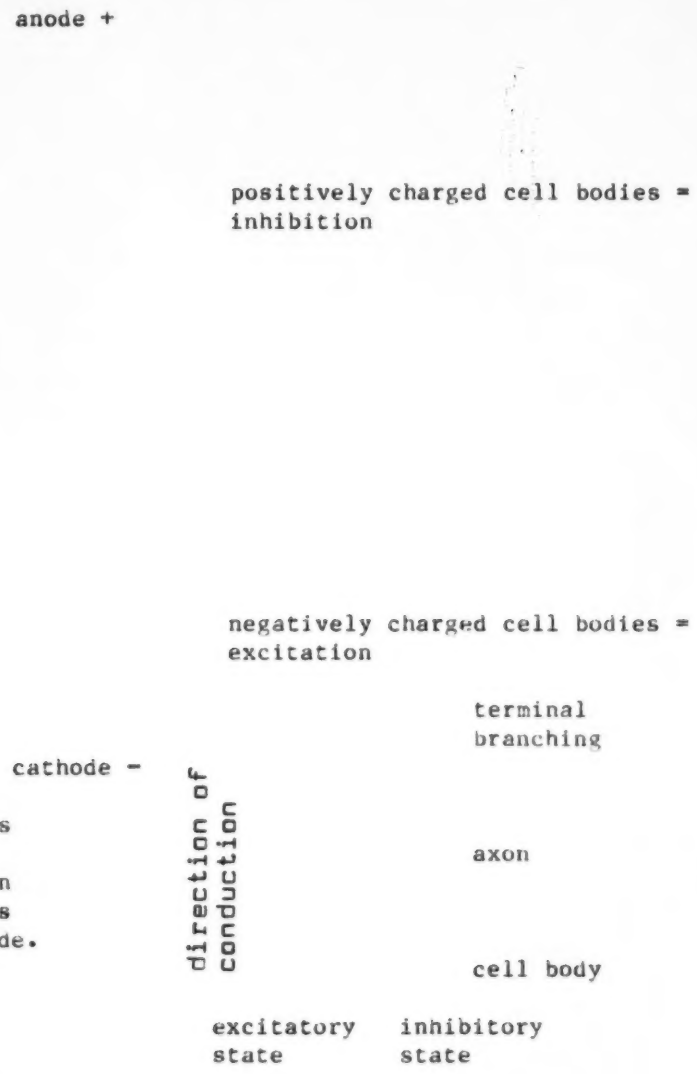

Fig. 4. Diagram of the nervous system of the fish from the brain to the posterior portion and polarization of the fibers when the animal faces the anode.

Spinal cord fibers: AB = sensory; CD = motor. Spinal nerve fibers: EF = sensory; GH = motor. Reflex centres: Rc = brain; Rs = spinal. Arrows indicate the direction in which the nerve impulses are propagated. Dark lines indicate excited fibers; regular lines, inhibited fibers. To the right, diagram showing the excitatory and inhibitory states of a nerve fiber. The impulse travels only if the cell body is negatively charged.

(threshold)

lack of excitation excitation

Fig. 5. The intensity of excitation or inhibition of a nerve fiber by an electric field depends on the potential difference between its extremities (cell body at the bottom, terminal branching at the top).

The intensity of excitation is shown by the thickness of the line representing the nerve fiber. Once the threshold of excitability has been reached, the isolated nerve cell responds by a constant level of excitation (all or none law). Since a nerve is made up of a bundle of fibers, the increase in excitation is due to the greater number of fibers that have been activated.

lack of excitation excitation

lack of excitation excitation

Fig. 6. The potential difference between the extremities of a nerve fiber placed in an electric field depends on the length of the fiber as well as its position in the field.

Same symbols as in Fig. 5. If the direction of the flow of current were reversed, then inhibition would naturally occur, instead of excitation.

only to the brain, and the motor chain only in the opposite direction. Excitation of tract AB produces a reflex in the brain that activates tract CD. Under ordinary conditions, this reflex which is coordinated in the central nervous system results in integrated muscle action as seen in a swimming pattern we refer to as 'normal' (Fig. 7) or in behaviour that is adapted to the circumstances.

Normal swimming pattern

Normal swimming pattern

Fig. 7. Normal swimming pattern in trout (top) and eel (bottom)
A normal swimming pattern in the absence of current is easily obtained by mechanically stimulating the tail.

Inhibited swimming pattern

Fig. 8. Facing the anode: inhibition of swimming
The absence of any churning in the water indicates that a voltage of 14 V considerably weakens or totally inhibits the animal's ability to swim. Compare with the normal swimming pattern (Fig. 7) and forced swimming pattern (Fig. 9).

Forced swimming pattern

Forced swimming pattern

Fig. 9. Facing the anode: forced swimming pattern
Note the amplitude and vigour of the well-coordinated movements.

Narcosis

Narcosis

Fig. 10. Facing the anode: narcosis with 40 volts.
The fish remains limp and motionless.

Pseudo-forced swimming

Pseudo-forced swimming

Fig. 11. Facing the anode: Pseudo-forced swimming.
Once the narcotic stage over, the fish begins to swim once more, but in an erratic, restricted fashion and for a short period of time. The swimming pattern is more sustained in the case of the common wild trout than in rainbow trout or eels.

Tetany facing the anode

Fig. 12. Facing the anode: tetany induced by 150 V

Fig. 13. Cathode galvanotaxis in trout.
The fish swims unsteadily toward the cathode. The movements are more restricted than in forced swimming with the animal facing the anode. An onset of stiffness when the voltage is increased indicates that tetany occurs at much lower voltages than in the case of animals facing the anode.

Tetany facing the cathode

Fig. 14. Tetany in the eel facing the cathode.
Tetany is induced at a much lower voltage than when the animal faces the anode (see Fig. 12).

Electrophysiology teaches us that when a nerve cell is placed in an electric field, excitation occurs if the cell body is placed toward the cathode. In this situation, the cell body is negatively charged (Fig. 4). Inhibition of the nerve fiber, i.e. absence of transmission of normal impulses, occurs when the position is reversed and the cell body is positively charged. Consequently, when the fish faces the anode, sensory tract AB is in an excitatory position, whereas motor tract CD is in an inhibitory position. Conversely, when the fish faces the cathode, tract AB is in an inhibitory position and tract CD, in an excitatory position.

The degree of excitation or inhibition of a nerve fiber depends on the potential difference between the extremities. A certain minimal potential difference is needed for the reaction to occur. This is referred to as the reaction threshold (Fig. 5). In a given electric field, however, the potential difference that is set up between the ends of a nerve fiber obviously depends on the length of that fiber. Thus, in the case of Fig. 6 (top), the difference is 2 V for AB, 4 V for DC and 6 V for EF. In the same electric field, long fibers are more readily excited than short ones, which have a higher excitation threshold. This means that large fish with longer nerve fibers will display a higher degree of excitability. It is also clear that an increased slant in the position of the nerve fiber in the field reduces the degree of excitation (Fig. 6, bottom). When the fiber is perpendicular to the field, there is no longer any potential difference between the extremities.

It should be pointed out that in a nerve tract (like sensory tract AB in Fig. 4), each fiber acts as if isolated from the next one. Continued transmission of the impulse along the tract is ensured at the synapse (the point of contact of the terminal endings of one fiber with the cell body of

of the next one) through chemical mediators. It is therefore not the potential difference between the two ends of a nerve tract that must be taken into account, but the difference between the ends of each one of its elements. Thus, tract AB, which is made up of short fibers, is much less readily excited that a single fiber of the same length.

These principles help to elucidate why, when a fish is placed parallel to the field and the potential is raised, excitation or inhibition occurs first in the long spinal motor pathways CD, then in sensory pathways AB, which are made up of short fibers, and lastly in spinal nerve pathways EF and GH, which are both short and slanting in the field (Fig. 4). If the animal is pivoted so that it lies perpendicular to the field, pathways AB and CD are no longer either excited or inhibited and the potential for excitation or inhibition of spinal nerve pathways EF and GH is increased.

Facing the Anode: Inhibition, Forced Swimming, Narcosis, Pseudo-Forced Swimming, Tetany

We refer once again to Fig. 4. With the fish facing the anode, sensory tract AB is in an excitatory position and motor tract CD, in an inhibitory position. We shall now discuss the behaviour of the fish when the potential between the head and the tail is gradually increased.

Excitation of sensory tract AB does not yet occur when the potential difference is low (14 V in the case of Table I) since the tract is composed of fibers that are too short for the excitation threshold to be reached. Motor tract CD, on the other hand, which is made up of long fibers, can be inhibited. Impulses from the brain which initiate and organize the animal's movements have to overcome this inhibition. With this potential difference,

inhibition is minimal and the motor activity of the fish is merely slowed down. This is what we referred to as the 'inhibited swimming pattern' (Fig. 8).

With a stronger voltage (18 V), the excitation threshold of fibers AB is reached. The stimulated tract then activates the brain structures which are too short for the electric field to act on them directly. These structures initiate a reflex. With the increase in potential, there is also a corresponding increase in the inhibition of motor pathway CD. While the brain reflex comes up against this inhibition, the latter is not yet strong enough at 18 V to prevent completion of the reflex (which triggers real expenditure of energy by the brain). The negative charges which accumulate through this process at extremity C of tract CD can still neutralize and exceed the value of the positive charges which the electric field has created. Excitation of tract CD is reflected in the behaviour by a harmonious and integrated swimming pattern resulting from coordination by the brain. This 'forced swimming pattern' is particularly fast and effective (Fig. 9).

If the voltage is raised still further, there is heightened excitation of sensory tract AB. At the same time, however, inhibition of motor tract CD increases proportionately, and there comes a moment when the reflex (limited amount) is no longer capable of overcoming this inhibition. From that moment on, the motor pathways are no longer activated by messages from the brain and the fish remains motionless. It is flaccid, for it is in a state of narcosis (Fig. 10).

Up to now, we have mentioned only the spinal sensory and motor pathways. Fig. 4 shows there is another tract between the periphery and spinal cord,

i.e., the spinal nerve pathway. Sensory spinal nerve EF and spinal nerve GH lie obliquely toward the posterior end of the body. Sensory spinal nerve EF excites motor spinal nerve GH via a reflex relay. This reflex occurs independently of the brain. It is a spinal reflex.

As in the case of the spinal tracts, when the fish faces the anode, sensory spinal nerve EF is in an excitatory position and motor spinal nerve GH, in an inhibitory position (except for the peripheral end which curves anteriorly). The same mechanism we described for the spinal pathways applies to the spinal nerves, but as the latter are shorter and lie obliquely in the electric field, much higher voltages are required (90 V for the reactions in Table I). Simultaneous excitation of all the sensory spinal nerves eventually gives rise to a swimming pattern involving the integration of spinal reflexes by the spinal cord which has the ability to coordinate reflex activity. As the brain can no longer intervene, however, because inhibition of CD is too great, the swimming pattern is disrupted and becomes erratic. This is due to some considerable degree of disarray in the motor impulses causing stiffness in the animal's body. We have called this type of swimming pattern 'pseudo-forced swimming' to distinguish it from forced swimming with which it has nothing in comon except the orientation of the fish (Fig. 11). It is very important to remember that as the voltage is increased, narcosis separates these two swimming patterns. It may therefore be concluded that they result from the excitation of different structures.

When voltage is increased still further, very short muscle fibers lying along the animal's longitudinal axis are stimulated directly, causing generalized stiffness or tetany (Fig. 12).

Facing the Cathode: Stimulated Swimming, Then Rapid Tetany

We shall now examine what happens when the fish faces the cathode. This time the sensory fibers of the spinal cord are in an inhibitory position and the motor fibers, in an excitatory position.

Low voltages of up to 14 V, which inhibit swimming when the fish faces the anode, cause direct excitation of the motor tract. The sensory tract, however, is made up of short fibers and is not yet inhibited. The brain sends out messages following various types of stimulation, other than electric, from the environment and these messages may continue to exert a coordinating effect on the motor pathway. Direct excitation of this pathway, still regulated by the brain, results in the production of a normal swimming pattern with only the speed enhanced. This phenomenon has been given the name of 'cathode galvanotaxis' (Fig. 13) which, as mentioned earlier, has been overlooked by many authors.

When the electric potential is increased to 20 V, direct excitation of the motor pathway overrides all else and is too great for the brain to continue to exert a regulatory effect. The swimming pattern becomes shaky, progressing toward an increasingly pronounced tetany as the voltage is raised (Fig. 14.). The phenomenon is all the more acute as excitation of the spinal motor pathway is attended by excitation of the motor spinal nerves, then of the muscle fibers themselves.

As may be seen, when the fish faces the cathode, the reactions resulting from direct excitation of the motor system by the current are far less complex than those produced by reflex excitation which occur when the fish faces the anode. In addition, tetany is achieved by much lower voltages in fish facing the cathode.

Anode Flexure

Imagine now that the fish is placed perpendicular to the current. As mentioned earlier, only spinal nerves EF and GH (Fig. 4) are affected by a potential difference between their extremities. If, for instance, the left side faces the anode, the motor spinal nerves on the left side are in a position of direct excitation, whereas those on the right side, facing the cathode, are in an inhibitory position. In the case of the sensory nerves, the converse holds true. A spinal reflex would therefore tend to occur on the right side, but it would be impeded by inhibition of the motor nerves. With direct excitation of the motor nerves on the left side, there is generalized contraction of the muscles on that side. The fish then curves with the extremities of the body facing the anode. This phenomenon has been called 'anode flexure.' It is produced by slightly lower voltage than is used to induce pseudo-forced swimming.

To jump ahead to experiments that will be discussed later (Table II), anode flexure is also achieved if the fish is decapitated and pithed by passing a metal wire in the neural canal (Fig. 15). This serves as evidence that there is direct excitation of the motor spinal nerves since all spinal reflexes are lost. Further evidence is provided by the following experiment.

Since a long nerve fiber requires less current to achieve excitation than a short fiber, it may be assumed that in animals with longer spinal nerves on one side of the body than on the other, less current will be required to produce flexure on the side with the longer nerves. This has been substantiated in animals with this peculiarity, i.e., the sole and amphioxus.

In the sole, the anode flexure threshold is 10 V for the left side and 7 V for the right. In the amphioxus, it is 37 V and 58 V, respectively (Fig. 16).

Fig. 15. Anode flexure in the demyelinated eel.
The animal was pithed by passing a metal wire into the neural canal. Once the current was established, the body curved with its extremities facing the anode.

anode flexure threshold 10 V	anode flexure threshold 7 V-37 V	anode flexure threshold 58 V

Fig. 16. Influence of spinal nerve length on anode flexure thresholds.
As may be noted, less voltage is needed on the side of the longer nerves. In addition, the discrepancy in thresholds is greater in the amphioxus (37 V on the left and 58 V on the right) than in the sole (7 V on the right and 10 V on the left) because of the greater disproportion in the length of the nerves between the two sides.

At voltages inducing anode flexure, the latter also plays a role in anode galvanotaxis. The fish undergoes a succession of flexures, bending alternately to the left and right, with the result that the fish is maintained within the axis of the field with its head facing the anode.

One other observation substantiates our general interpretation of the nervous mechanisms involved. In our discussion thus far, we have neglected to mention the extreme anterior portion of the fish, between the brain and snout. The polarity of the sensory and motor nerves is obviously the reverse of that found in the rest of the body. This means that reflex activity should be observed when the animal faces the cathode and motor activity when it faces the anode, i.e., the opposite of what occurs in the portion posterior to the brain. This is exactly what was recorded in eye, mouth and gill cover movements. Reflex movements appeared suddenly and were short-lived, whereas direct effects were prolonged and sustained.

TABLE 2. BEHAVIOUR RELATED TO INCREASES IN POTENTIAL AND SECTIONING OF THE CENTRAL NERVOUS SYSTEM AT DIFFERENT LEVELS

		fish facing the anode						fish facing the cathode				fish perpendicular to the field	
Levels of sectioning the central nervous system		inhibited swimming pattern 14 V Fig. 8	forced swimming 18 V Fig. 9	narcosis 40 V Fig. 10	pseudo-forced swimming 90 V Fig. 11	tetany of nerves 90 V	tetany of muscles 150 V Fig. 12	cathode galvano-taxis 14 V Fig. 13	tetany of nerves 20 V	tetany of nerves 40 V Fig. 14	tetany of muscles 150 V	anode flexure Fig. 15	
		1	2	3	4	5	6	7	8	9	10	11	
telencephalon	A intact fish	+	+	+	+	+	+	+	+	+	+	+	A
	SECTION 1												
mesencephalon / cerebellum	B cerebello-mesencephalic fish	+	+	+	+	+	+	+	+	+	+	+	B
	SECTION 2												
medulla	C medullar fish	+ lowered threshold	−	+ lowered threshold	+	+	+	+ lowered threshold	+	+	+	+	C
	SECTION 3												
	D spinal fish		−		+	+	+	+	+	+	+	+	D
	DESTRUCTION												
	E demyelinated fish		−		−	+	+	−	−	+	+	+	E
	CURARIZATION												
	F curarized fish		−		−	−	+	−	−	−	+	−	F

Discussion of Table II

Regardless of where the nervous system of the fish is sectioned, the portions located below the section remain intact. The fish in the diagram has been labelled according to the highest level of preserved nervous function. The 'medullary fish', for instance, refers to a specimen in which the medulla oblongata is intact. A 'spinal' fish is one in which only the spinal cord has been preserved (along with the spinal nerves to which it gives rise, of course).

\+ = positive reaction for the electric voltage indicated

\- = suppressed reaction.

Lines A and B. Since the telencephalon is primarily an olfactory centre, suppression of this part of the brain does not interfere with any of the reactions.

Line C. Without the regulatory effect of higher structures which are responsible for some resistance to the electric current, the thresholds of certain reactions (inhibition of swimming, narcosis, cathode galvanotaxis) are lowered in the medullary fish which swims non-stop. Furthermore, in the absence of the cerebellum the fish swims erratically.

Lines D, E, F. Any section below the medulla results in immobility of the spinal fish when left to itself. It is no longer possible to study inhibition of swimming or narcosis which represent the slowing or cessation of spontaneous movements involving the structures that have been destroyed. The corresponding boxes in the table have consequently been marked off with hatching.

Column 2. Forced swimming must originate in the mesencephalon/cerebellum since it is not observed in medullary fish.

Column 4. Since pseudo-forced swimming is produced by spinal reflexes (sensory spinal nerves in a excitatory position) that have been integrated by the spinal cord, it no longer occurs after destruction of the cord.

Column 5. The tetany induced by 90 V which accompanies pseudo-forced swimming disappears only under the effect of curarization. It results from excitation of the curved peripheral ends of the motor spinal nerves (not shown in Fig. 4).

Columns 6 and 10. Since tetany induced by 150 V in both directions of the current persists in curarized specimens, it must result from direct excitation of the muscles.

Columns 7, 8, 9. Tetany induced by 20 V is produced by increased excitation of the spinal motor tract resulting in cathode galvanotaxis. The brain is no longer capable of regulating this degree of excitation. Tetany, like cathode galvanotaxis, disappears once the spinal cord has been destroyed. Tetany produced by 40 V, on the other hand, is due to excitation of the motor spinal nerves and does not disappear until after curarization. The lower threshold for cathode galvanotaxis that has been observed in medullary fish indicates that all resistance from the higher centres has been abolished.

Column 10. With a voltage of 150 V, tetany is the result of direct excitation of the muscles and persists in curarized specimens.

Column 11. Anode flexure, which is dependent on motor spinal nerves, disappears only after curarization.

Octopus and Dragonfly Larva

The functional outline we have given should make it possible to predict in which direction galvanotaxis will occur in an animal in which the mode of locomotion and orientation of the nervous system are known. An octopus, for instance, normally moves by contracting the mantle cavity which expels water forward, propelling the animal backward. A dragonfly larva, on the other hand, moves by contracting the rectal ampulla which sends water backward, propelling the animal forward. It has also been clearly demonstrated that the motor nerves of these two animals extend from centres located anteriorly to the rear portion of the body.

If both animals are placed facing the cathode so that the motor pathways are in an excitatory position, it may be assumed that contraction of the mantle cavity in the octopus as a result of excitation of its motor nervous system will make it move backward toward the anode and that contraction of the rectal ampulla in the dragonfly larva, arising from the same mechanism, will make it move toward the cathode. This hypothesis has been experimentally substantiated (Fig. 17), demonstrating that the direction of galvanotaxis in an electric field depends on the orientation of the nerve fibers in the field as well as the mode of locomotion in the animal. The effects may consequently be different in different animals.

While the sensory pathways undergoing excitation when the animal faces the anode have not been systematically studied because their anatomy is still poorly understood, it should be mentioned that when in this position, the octopus tries to anchor itself to the bottom of the tank. This corresponds to its ecological behaviour when disturbed.

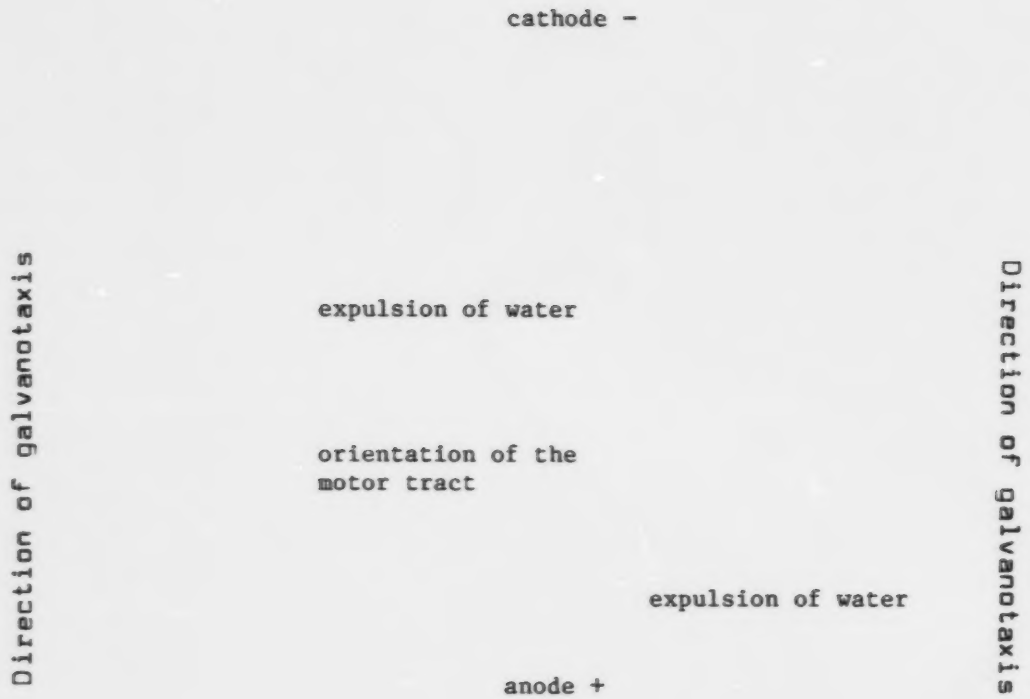

Fig. 17. Diagram of galvanotaxis in an octopus (left) and a dragonfly larva (right), both facing the cathode.
The motor tracts of both animals are oriented in the same direction, but the expulsion of water which enables them to move occurs in opposite directions, explaining why galvanotaxis also occurs in opposite directions.

Procedures Involving the Central Nervous System

The interpretations we have given called for more extensive experimental substantiation. First of all, sections were made at various levels in the central nervous system of fish specimens. With each section, the portions of the system above the section could no longer exert any effect, whereas the areas below the section continued to function (Table II).

When an animal is deprived of its telencephalon, it is said to be 'cerebellomesencephalic' since the cerebellum and mesencephalon represent the highest nervous structures it still retains. Likewise, the expressions

'medullary fish' and 'spinal fish' indicate at what nervous level the animal can operate. The demyelinated animal is deprived of its spinal cord by the method described earlier. Curarization, obtained by intramuscular injections of D-turbocurarine until total inertia is achieved, prevents the transmission of any nerve impulses. Only direct stimulation of the muscle by the electric current is capable of producing an effect. Table II summarizes these various procedures with their attendant results when the fish is placed in different positions in an electric field with different voltages. From the caption under the table it may be seen that the results support our hypotheses.

The use of anesthetics also provided conclusive evidence. If forced swimming is truly the only reaction studied that is triggered by a cerebellomesencephalic reflex, then it should no longer occur in urethane-anesthetized fish, since urethane electively inhibits brain activity. All the other reactions should be preserved. This hypothesis proved correct. Both ether and xylocaine, on the other hand, paralyse all sensory pathways. It may then be assumed that they will abolish forced swimming and pseudo-forced swimming which are produced by these reflexes, forced swimming by excitation of the spinal sensory tract and pseudo-forced swimming by excitation of the sensory spinal nerves. These two swimming patterns were generally abolished. In cases where they did persist, however, they were considerably depressed, whereas the thresholds of the other reactions remained normal.

The abolition of forced swimming following the injection of xylocaine into the spinal cord provided further evidence that in this type of swimming pattern, sensory nerve impulses were transmitted by the spinal pathway. In order to eliminate any doubt, three other possibilities had to be ruled out:

direct excitation of the brain by the current, transmission by the lateral line or by the vagus nerve. Since forced swimming persisted despite sectioning of the lateral line and the vagus nerve, the possibility of transmission by these two pathways could quickly be discarded.

In order to eliminate the hypothesis of direct excitation of the brain by the current, medical fingers were placed over the heads of eels to insulate them against the current. The rest of the body, however, was exposed to current activity. It was found that the threshold for forced swimming was not modified. We also sent a concentrated flow of current into the telencephalon of a large eel. For this experiment, the animal was trepanned and an electrode placed in contact with the telencephalon. It was connected to a radio battery attached to the animal's back. The circuit was closed by an electrode placed around the body. The wounds were sewn up and electrically insulated using dental varnish. A few days after the eel had resumed normal activity, the battery was connected but it was not possible to trigger a forced swimming pattern, even when the battery was connected in series with another battery, then with a dynamo. It may be concluded that only the spinal pathway is involved in forced swimming.

Role of Animal Psychology

The explanations we have proposed were based on findings recorded in 23 animal species, including 17 fish species. These animals were selected on account of differences in anatomy, modes of locomotion and natural behaviour. Because of the range of experimental subjects, we were able to observe interesting differences which warrant a brief discussion.

There is far more uniformity in reactions among species, as well as within the same species, when the higher centres do not come into play, either because they have been destroyed, or else because of the reaction mechanisms involved, as in the case of pseudo-forced swimming. Mention should be made here of the following experiment. When a cuttlefish was placed across an electric field of a given voltage, it underwent the colour changes shown in Fig. 18, i.e., the side of the head facing the cathode turned black, whereas the mantle on that side lost all pigmentation. The side of the head facing the anode, on the other hand, became white, whereas the mantle turned black. These colour changes resulted from excitation of the sympathetic system and reflect the structure of the system. In such instances, animal psychology obviously cannot be implicated.

In other instances where brain reflexes are intact, the reactions of the fish are largely modified by its normal ecological behaviour. When an eel, for instance, is placed in the experimental tank where it cannot hide, it reacts by entering a state of forced swimming (Fig. 9). Under conditions of electrofishing, however, an eel can anchor itself under the bank where it is hiding. Voltages capable of initiating forced swimming elicit instead an anchor response in the brain and the animal can be caught only when the electrode is brought close enough to produce voltages capable of inducing a pseudo-forced swimming response, the higher nerve centres no longer being involved.

Naturally, reactions like forced swimming or anchoring hinge on behaviour that clearly cannot be repressed, and the main reactions can no longer be explained in terms of psychological mechanisms. The animal, however, can display some degree of resistance, which might even be considered of

psychological origin since it is linked to the integrity of the higher nerve centres. As may be seen in Table II, the threshold of certain reactions , i.e., inhibited swimming, narcosis, cathode galvanotaxis, is lowered by destroying the structures above the medulla. As long as the cerebellum and mesencephalon remain intact, the animal retains some capacity to "oppose" the constraint placed upon it.

In this regard, mention should be made of one last experiment in trout. Voltages capable of inducing forced swimming in trout (18 V) could no longer elicit the response when the voltage was gradually built up. In this case, a much higher potential difference (26 V between the ends of the experimental tank) was needed for the reaction to occur. These findings suggest that the fish had time to adapt to new conditions and develop better resistance to the stimulus. It was then hypothesized that the trout had an "action-acceptance centre" in the brain that exerted some degree of control on the reflex centre (the cerebellomesencephalic centre) for forced swimming. It was further hypothesized that this higher centre must be less resistant to interference than the reflex center which it regulates. We then began experiments with trout that had previously received electric shock with alternating current on the assumption that these shocks would neutralize the "action-acceptance centre" without abolishing the cerebellomesencephalic reflex. In the fish given electric shocks, it was shown that forced swimming was initiated with as little as 15 V, regardless of whether this voltage was administered at once or in gradual increments.

Table II also shows that fish offer some resistance of encephalic origin to other types of excitation or inhibition (cathode galvanotaxis and narcosis) since destruction of the brain lowers the thresholds of these reactions.

Fig. 18. Electric excitation of the sympathetic nervous system in cuttlefish.
With the same potential difference, only the direction of the current influences pigmentation of the various areas of the body in the cephalopod.

Fig. 19. Catching young trout by means of electrofishing in a stream in the Basses-Pyrénées.

While it is true that the behaviour of fish in an electric field cannot be explained in psycological terms, it is also true that the animals are not always the simple playthings of their environments. Galvanotaxis, involving either electrode, occurs only insofar as the fish can no longer control direct excitation of its nervous system. It would be interesting to conduct a systematic study of the resistance capacity of various aquatic species in which a substantial difference exists in the degree of development of the brain structures. A study of this type would be of practical as well as theoretical value. It may be assumed, for instance, that animals at the lower end of the evolutionary scale will very rapidly enter a state of narcosis when facing the anode and display signs of cathode galvanotaxis at low voltages. This would prove highly beneficial for any electrofishing involving these species.

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Fig. 1

Fig. 2

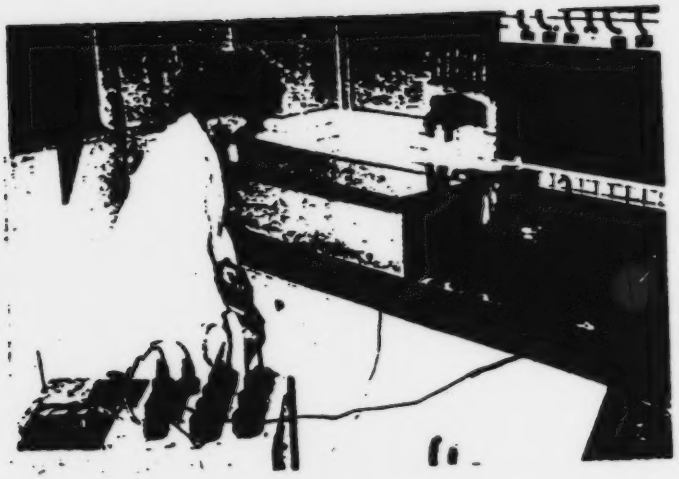

Fig. 3

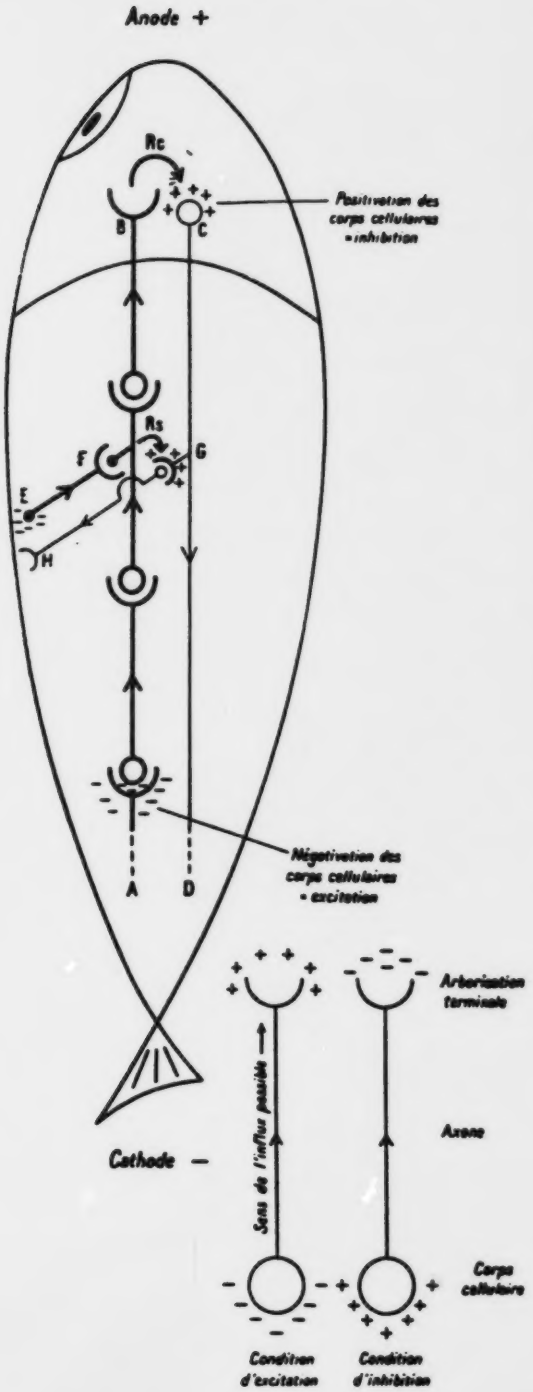

Fig. 4

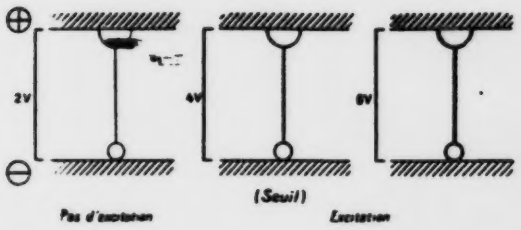

Fig. 5

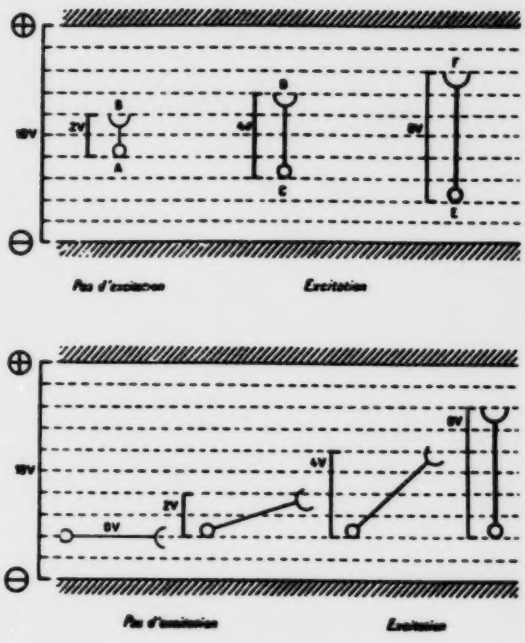

Fig. 6

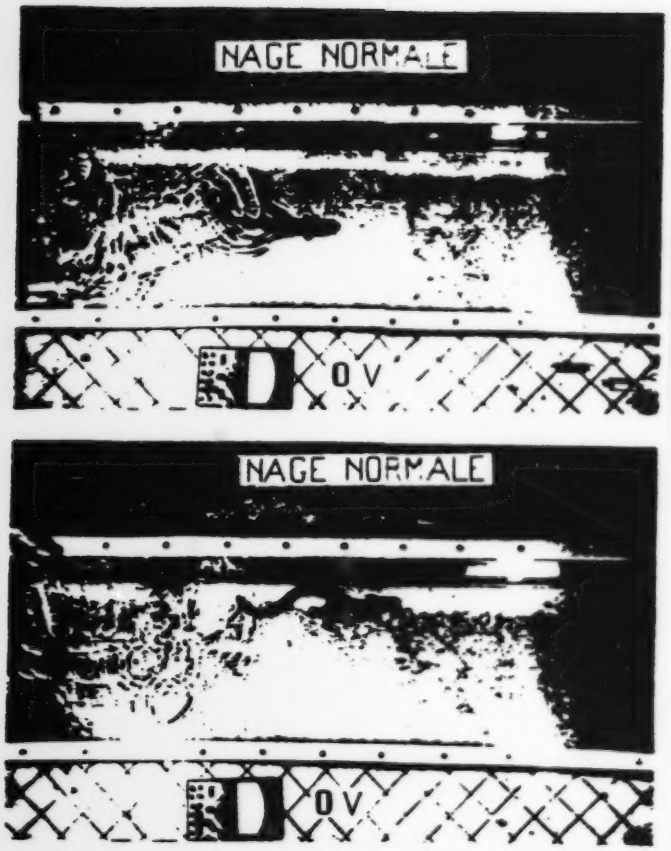

Fig. 7

Fig. 9

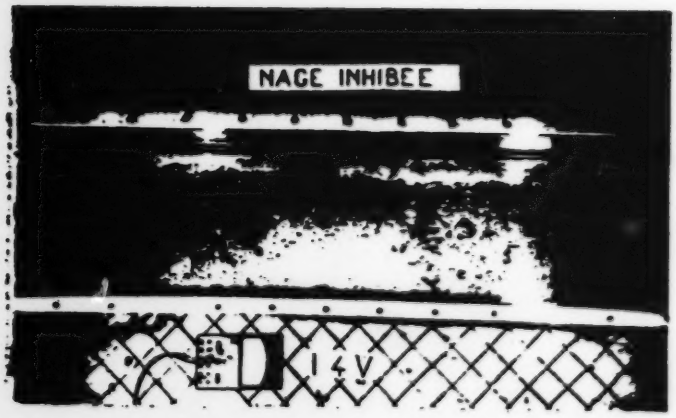

Fig. 8

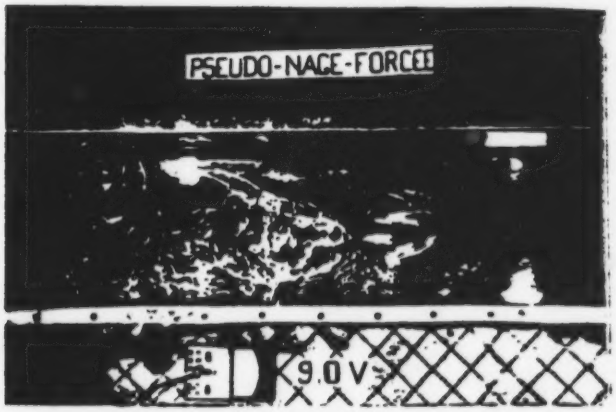

Fig. 10

Fig. 11

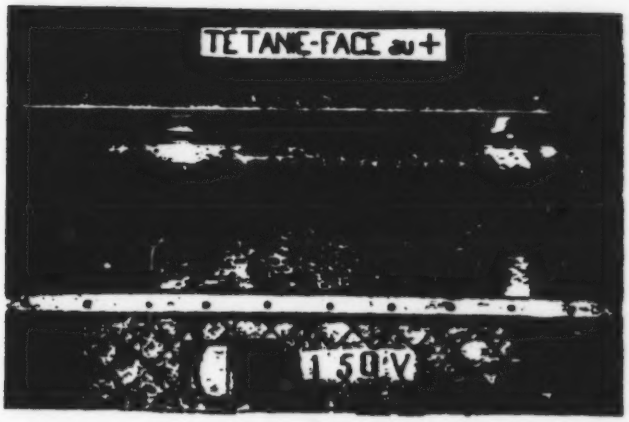

Fig. 12

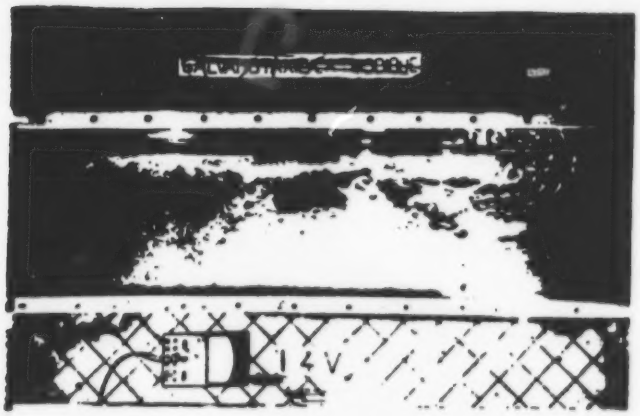

Fig. 13

Fig. 14

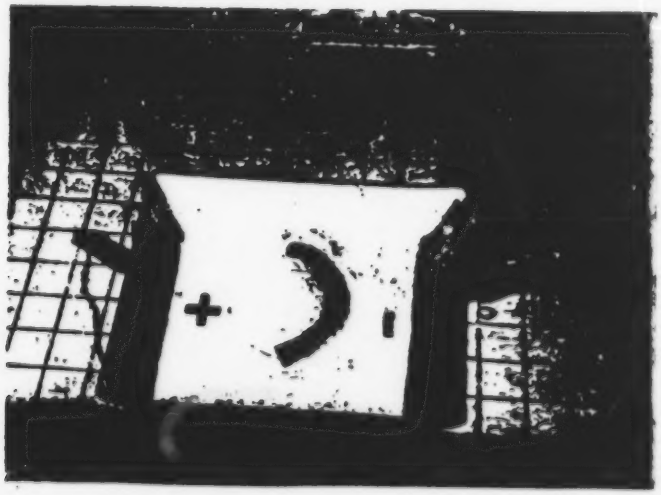

Fig. 15

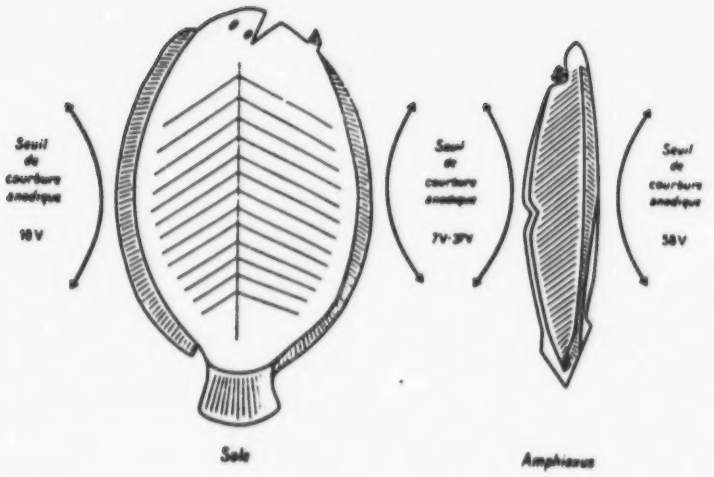
Seuil de courbure anodique
10 V
Seuil de courbure anodique
7V-37V
Seuil de courbure anodique
58V
Sole
Amphioxus

Fig. 16

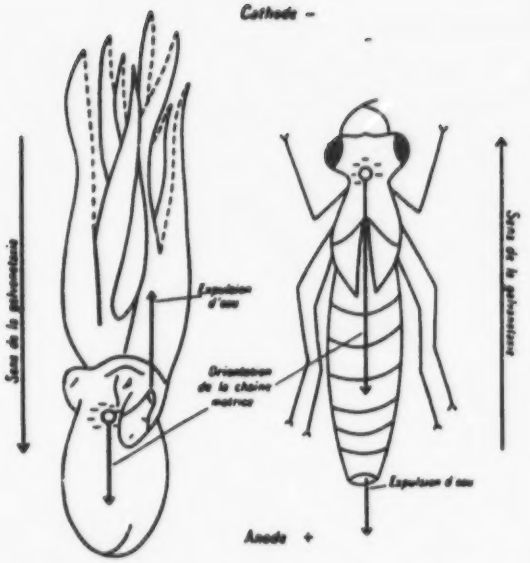
Cathode -
Sens de la galvanotaxie
Expulsion d'eau
Orientation de la chaine motrice
Sens de la galvanotaxie
Expulsion d'eau
Anode +

Fig. 17

Fig. 18

Fig. 19